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Patch use of Winter Resident and Migrant American Kestrels (Falco sparverius) in the Coastal Plain of Virginia

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Patch use of winter resident and migrant American Kestrels (*Falco sparverius*) in the Coastal Plain of Virginia

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by

Rhonda Lynn Hardesty Sipe

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APPROVAL SHEET

This thesis is submitted in partial fulfillment of

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Approved, April 2002

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ABSTRACT

American Kestrels (*Falco sparverius*) are common throughout the Coastal Plain of Virginia except during the summer breeding season. Eight survey routes consisting of eighty-six 10 km road segments that varied according to the amount of available open habitat were surveyed by automobile. A total of 463 birds were recorded with an overall sex ratio of 58.9% males and 41.1% females. Winter surveys showed a skewed sex ratio favoring males, as did surveys conducted during spring migration. However, when divided into early and late survey rounds, spring sex ratio data supported differential timing of migration by sex, with males moving through earlier than females.

Male and female kestrels exhibited similar patterns of habitat use during all seasons. Kestrels were found to use both agriculture and idle grass areas significantly more than expected, while pasture, forest, and 'other' habitats were used significantly less than expected. Residential areas and clear-cuts were used according to their availability. Kestrels occupied much larger agricultural patches in winter compared to those occupied during migration. Small agricultural patches that were imbedded within landscapes containing open habitat complexes had a significantly higher probability of being occupied compared to isolated patches. Occupation rates were influenced during both winter and migration by the proportion of open habitat within a survey segment. This was a significant relationship in winter with the highest occupation rates occurring in areas with open habitats accounting for more than 70% of the landscape. A similar trend was observed in the migration period but was not statistically significant. Kestrel density showed a positive response across the landscape gradient in winter with an average density more than twice as high along segments with > 70% open habitat. Average density within the migration periods showed no detectable trend across the landscape gradient.

Kestrels in the Coastal Plain of Virginia showed a similar sex ratio and no differential habitat use between the sexes, which support similar findings at this latitude in Kentucky. Densities of kestrels within the study area seemed to be much higher than reports in other studies, with 0.41 observations/100 ha for open habitats in winter, 0.64/100 ha in spring, and 0.35/100 ha in fall.

Selection of habitat patches of greater size than predicted from the range of sizes available has not been demonstrated previously. It follows logically that kestrels would select patches using different criteria under varying seasonal conditions. This is supported by wintering kestrels rarely being sighted in agricultural patches with less than 800 m of road frontage. In contrast, these patches were used with some frequency during migratory periods.

PATCH USE OF WINTER RESIDENT AND MIGRANT AMERICAN KESTRELS

(*FALCO SPARVERIUS*) IN THE COASTAL PLAIN OF VIRGINIA

INTRODUCTION

A localized study of American Kestrels (*Falco sparverius*) in the Coastal Plain of Virginia is necessary because other than nationwide surveys such as the Christmas Bird Count and the Breeding Bird Survey, little research has been conducted on this kestrel population. The specific objectives of the present study will be to: determine density and sex ratio of migratory and wintering Coastal Plain kestrels, investigate use of land cover in relation to availability of cover types, compare patch size use between seasons, and describe landscape use based on proportion of open area at local and broad scales.

The American Kestrel, formerly called the Sparrow Hawk, is North America's smallest falcon. The species ranges over most of North and South America. American Kestrels are common transients and winter residents in the Coastal Plain of Virginia. The species is sexually dimorphic in size and plumage color. Birds stand from 23 to 30 cm tall; males weigh 103 g on average, females 120 g (Bird 1988).

The habitat occupied by kestrels is typically open terrain such as farmland, fields, urban areas, woodland edges, plains, deserts, and roadsides (Bird 1988; Balgooyen 1989). In Jamaica, birds were observed in cultivated areas, coconut and citrus groves, wooded pasture, woodland savannahs, scrub woodland, and suburban areas (Cruz 1976). Of 6,359 foraging sites in Boone Co., Missouri, disturbed grasses were over-utilized, croplands and woodlots under-utilized, and old fields, idle grass, and plowed fields utilized as expected based on percentage habitat availability (Toland 1987). In comparison, kestrels in Madison Co., Kentucky, used pasture, old field, and cropland more often than expected by chance, and plowed fields, woodlots, and urban areas less often than expected by chance (Sferra 1984a).

The diet of American Kestrels includes insects, birds, small mammals, reptiles, and amphibians, and their main food source varies depending on season and locality. Perching is the predominant method of foraging, followed by hovering. Perching sites range from natural (rock outcrops, tree stumps, small shrubs, and dead trees) to artificial (telephone lines, fence-posts, and other manmade structures) (Bird 1988).

Kestrels may establish pair bonds and breeding territories as early as the beginning of March with egg laying occurring by the first week in May. Incubation takes place over approximately thirty days. Young are reared between late April and mid-August, and kestrels stay on wintering territories from August to March. Cade (1955) was the first to describe winter territoriality in kestrels following the dissolution of pair bonds.

American Kestrel population numbers have risen gradually in recent National Audubon Society Christmas Bird Counts and the Breeding Bird Survey (Stokes and Stokes 1996), but dramatic declines have been noted in certain areas. Kestrels have shown no adverse reaction to DDT in terms of population counts over the past 52 years at Hawk Mountain, Pennsylvania in contrast to several other species of raptors. However, from 1971 to 1986 there was a downward population trend due to conversion of pasturelands into residential developments and intensive row-crop agriculture in the northeastern United States (Bednarz 1990). An 85% historic decline in numbers has been observed in north central and south central Florida, due to loss of foraging and nesting habitat (Hoffman 1983). This has been attributed to clearing of isolated longleaf pine trees from agricultural fields, conversion of turkey-oak/longleaf sandhill to citrus groves, and changes in the understory of virgin pine forest through clearing and fire (Hoffman and Collopy 1988).

In summer on the Coastal Plain of Virginia, residents are uncommon and very little is known about the small population that is present. As of November 1993, the most recent year from which data are available, the Virginia Breeding Bird Atlas Project (a joint project between the Virginia Society of Ornithology and the State of Virginia) had only five confirmed breeding sites for American Kestrels in the coastal plain. There were additional sightings of summering kestrels but no nest sites were found. It is possible that some year-round residents occur in this area, but the large majority of the kestrel population migrates through in the fall and spring. Haugh (1972) found that females precede males during the fall migration in the Great Lakes area. Smallwood (1988) found that males arrived later on winter territories in south central Florida. Stotz and Goodrich (1989) detailed differential timing of migration by sex at Hawk Mountain, Pennsylvania, from 1963-1988. On average, females preceded males by 11 days during fall migration. Other studies (Roest 1957; Smith *et al.* 1972) suggest that males move through earlier during spring migration in order to compete for and establish high-quality breeding territories.

Reports of sex ratios have varied considerably in different localities. Roest (1957) stated that males made up 60% of summer, fall, and winter kestrel populations across a wide area of the United States. Smallwood (1988) collected data on all kestrels of known age and sex banded east of 100° W longitude in North America in the months of September to November 1960-1984. His data indicated a ratio of 9,618 (52.4%) males to 8,749 (47.6%) females. Arnold (1991) compiled data from 152 National Audubon

Society Christmas Bird Count surveys in areas ranging from Wenatchee, Washington, to San Blas, Mexico. Of 4,043 birds identified by sex, 2,327 (57.6%) were males and 1,716 (42.4%) females. Sferra (1984a) documented a total of 365 sightings of wintering kestrels in Madison Co., Kentucky, with 212 (58%) males and 153 (42%) females.

Several authors (Willoughby and Cade 1964; Koplin 1973; Collopy 1973; Mills 1975, 1976) have described an unbalanced sex ratio in favor of females in wintering kestrels. This is often a localized effect found in conjunction with differential habitat preference. Koplin (1973) reported six to twenty times as many females as male kestrels wintering in some areas in California. Female kestrels were much more likely to be found in agricultural areas, while males made up the majority of sightings in forest and scrub habitats. The author interpreted this as character displacement reducing intersexual competition for food resources, that is, because males and females were not dimorphic enough in size to have differing food requirements, niche partitioning had occurred. Mills (1976) found a similar habitat preference in Arizona and northern Texas, but supported the female dominance theory, stating that larger females (8% greater mass, on average) were forcing males in sub-optimal habitats for foraging.

Stinson *et al.* (1981) observed a similar trend in kestrels wintering on a barrier island off of the coast of Georgia. These authors' interpretation was that the sexes possibly preferred different types of prey and were occupying separate ecological niches. Bohall-Wood and Collopy (1986) found that females preferred pasture areas and males preferred wooded areas in the winter, but that there were no sexual differences in habitat preference during summer months. Of 1,433 sightings in a population of wintering permanent residents in north central Florida, 65% were female and 35% male.

After noting that female kestrels preferred open areas such as pasture with short ground vegetation, Smallwood (1987) found that 60% of female habitat in south central Florida was covered by suitable hunting substrate, defined as grasses less than 25 cm in height. Males were more common along the perimeters of woodlots, citrus groves, and residential areas, and only 30% of their habitat had suitable hunting substrate. Smallwood (1988) went on to demonstrate that winter territories of high foraging quality were occupied first. Females, due to their earlier arrival on the wintering grounds, usually settled these areas. Observation of 650 territories convinced Smallwood that males and females were equally successful in territorial disputes; there was no evidence of displacement of males by females during the study period. Therefore, arrival date was the principal determinant of territorial holders within quality habitats. The delayed molt in adult males, due to reduced body mass from focus on feeding nestlings and brooding mates late in the breeding season, led to the differential timing of migration.

Ardia and Bildstein (1997) removed males and females from winter territories and observed reoccupation patterns. Female territories were more likely to be reoccupied than male territories, and female kestrels were more likely to occupy vacated female areas. The authors interpret this to indicate that females are capable of excluding males from higher quality sites. Ardia and Bildstein speculated that predation from other raptors, including Sharp-Shinned Hawks (*Accipiter striatus*), Northern Goshawks (*Accipiter gentilis*), and Cooper's Hawks (*Accipiter cooperii*), was less in open areas than along forest edges. According to these researchers, females choose more open areas because of the lower perceived predation risk. Males tend to eat a higher proportion of passerines, which are more available in semi-open areas. These authors concluded that a combination of male prey preference and exclusion of males by females results in the observed patterns of habitat use.

In Virginia, as in many areas of the eastern United States, major changes have occurred in proportions of available habitat over the last century. According to a study by the U.S. Department of Commerce (1981), open farmland declined 32% between 1945 and 1978, with much of the agricultural lands converted to other uses being taken from pasture, hayfields, and idle grassland. Total area of idle grasslands declined 55% over the same period. Shifts in agricultural methods resulting in more intensive use of remaining croplands have had negative impacts on a number of avian species (Millenbah *et al.* 1996). Grazing pressure on remaining pasturelands is becoming much more severe, with a 364% increase in cattle per acre of land over the 33-year period. These changes in human land use patterns are likely to be amplified as population growth continues in coastal areas. By 2010, it is predicted that coastal populations will have grown 60% from their already significant numbers (Cullitin *et al.* 1989).

Given the extreme impact of human land use on habitat patterns in the Coastal Plain of Virginia, this study seeks to characterize habitat requirements of wintering and migrating American Kestrels in relation to current availability of open patches and landscape context at fine and broad scales. Analysis of habitat patch use by both sexes was conducted at a scale of several hectares, incorporating intrinsic effects of patch and segment composition and the extrinisic effect of patch context on kestrel density and location.

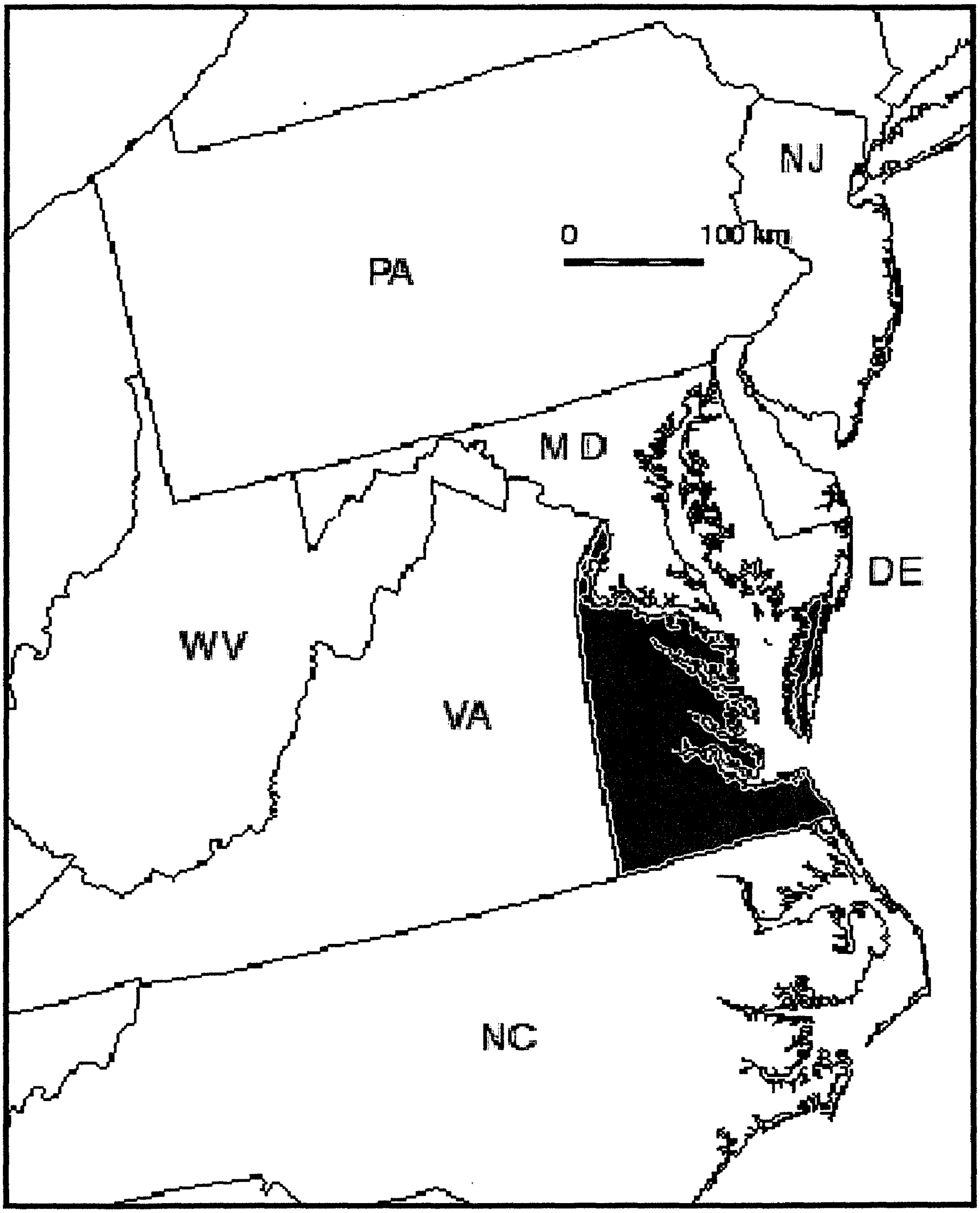
METHODS

Study Area

This study was conducted on the Coastal Plain of Virginia. For the purposes of this study, Coastal Plain refers to all areas east of Interstate 95 (between $36^{O}30'$ N and $38^{O}30'$ N latitude and $75^{O}30'$ W and $77^{O}30'$ W longitude) and consists of approximately 11,500 km^2. The Coastal Plain extends from the Fall Zone eastward to the Atlantic Ocean (Figure 1). The landscape was formed over the last few million years due to the rise and fall of sea level in response to the continental glaciers growing and retreating and the Coastal Plain itself slowly uplifting. Water is a dominant feature of the landscape with several large tidal rivers including the Potomac, Rappahannock, York, and James flowing southeastward across the Coastal Plain into the Chesapeake Bay, which in turn empties into the Atlantic Ocean. This drainage pattern has created salt marshes, forested wetlands, and barrier islands. The remaining portion of the Coastal Plain consists of upland forests from pine dominated areas on the outer edge (nearer to the coast) to inland hardwood forests. The Coastal Plain receives 117.5 cm of rainfall annually and has an average annual temperature of 13 to 14 degrees C.

In the fall of 1995, eight survey routes were selected. These were widely scattered and included a large portion of the total area of the Coastal Plain (Figure 2). A total of eighty-six roadway segments were chosen within the survey routes. All segments were 10 km in length and were selected based on proportion of open area shown on topographic maps 300 m to either side of the roadway segment. Open area surrounding roadway

Figure 1. The study area in the Coastal Plain of Virginia.



NJ
0
100 km
PA
MD
DE
WV
VA
NC

Figure 2. Enlarged map of Coastal Plain of Virginia with locations of eight survey routes indicated by number: 1) Eastern Shore, 2) Pungo, 3) Courtland, 4) Suffolk, 5) James River, 6) Fredricksburg, 7) Northern Neck, 8) Middle Peninsula.


6
7
8
5
3
4
2
1
Chesapeake Bay
Atlantic
Ocean

segments ranged from approximately 20% to 80% open landscape. Urban areas and interstate highways were avoided due to heavy traffic and reduced visibility. Number of roadway segments within each survey route ranged from 8 to 13 (Appendix 1). Proportions of open area were not evenly distributed among survey routes due to systematic shifts in land cover from the coast to further inland.

Road Surveys

American Kestrels were surveyed by driving along roadway segments at a speed of approximately 40 km/hr and visually scanning the surrounding landscape. Each segment was surveyed nine times between January and December 1996. The segments within a single route were always surveyed over the course of one day. Surveys were conducted between 9:00 and 15:00. No surveys were conducted during rain or snow. Surveys were conducted in rounds such that all eighty-six segments were completed once before starting a new round. The length of survey rounds varied between 8 and 14 days. Survey order of roadway segments within each route was alternated between rounds to remove any time-of-day bias.

Survey rounds were subdivided according to season. Three survey rounds were conducted during the winter, and two each during spring migration, summer breeding, and fall migration. Winter surveys were conducted from 18 January through 14 March. Surveys during spring migration were conducted between 20 March and 23 April. Breeding season surveys were conducted between 1 June and 10 July. Surveys during fall migration were conducted between 10 October and 26 November.

Location of each kestrel observed was plotted on the appropriate 7.5 minute topographic quadrangle. Several variables were recorded for each bird including gender and habitat type used. Habitat was categorized as forest, clear-cut, agriculture, pasture, idle grass, residential, and 'other' (Table 1). Forested areas were covered by trees over 2 m in height over greater than 50% of their area. Clear-cut areas were those from which the majority of trees had been harvested in the previous five years. Many of these areas contained small saplings and scattered dead trees. Agricultural areas were those routinely planted and cultivated. Pasture areas were usually fenced in and showed signs of recent use by livestock. Idle grasslands were tall grassy areas that were mowed less than 3 times per year, including highway medians and shoulders that were not forested. Residential included any grassy areas that were routinely manicured and kept low to the ground. The category 'other' was a catch-all for miscellaneous land cover types including buildings, waterways, and parking lots.

Habitat evaluation

Since topographic maps only display forested and open habitat, it was necessary to directly assess type of open habitat within the surrounding landscape for all roadway segments between 15 November and 15 December. This was done by driving each segment an additional time and recording habitat type on either side of the roadway at 0.1 km increments, with the assistance of an additional researcher or a tape recorder. Seven habitat types were quantified: forest, clear-cut, agriculture, pasture, idle grass, residential, and 'other' (Table 1). Habitat types were quantified within a 300 m band on either side of

Table 1. Habitat categories used during kestrel surveys.

Habitat types	Description
Forest	Over 50% of area covered with trees at least 2 m tall
Clear-cut	Trees removed in the past 5 years, saplings may be present but under 2 m tall
Agriculture	Areas are routinely farmed
Pasture	Usually a fenced-in area with low vegetation, signs of recent use by cattle
Idle Grass	Grassy areas mowed less than three times per year, includes highway shoulders and medians
Residential	Grassy areas kept low to the ground and frequently manicured
'Other'	All other areas including buildings, waterways, parking lots, etc.

roadway segments. Habitat information was compiled on acetate overlays by tracing the 600 m area around the roadway off 7.5 min topographic quadrangles and using a color-coding system to indicate habitat type within patches. Areas of target habitats were estimated from acetate overlays to the nearest 0.1 ha using an English-area grid. Areas of some idle grass patches, such as medians and road edges, were estimated and added to exact areas obtained from the English-area grid. Frequency distribution of kestrel observations among land cover types were obtained with expected values based on relative of availability of land cover type.

Patch Use

Land cover maps indicating habitat types were used to quantify the number, size, and structure of open patches along roadway segments. An electromagnetic digitizing tablet was used to measure the length of road frontage for all open habitat patches to the nearest 10 m. A patch was a unit of habitat defined as the length of homogeneous land cover with the boundary set at the transition point into another type of habitat. The underlying assumption is that length of road frontage is related to overall patch size since the roadway transects the patch. Average patch size was calculated for winter and migration along with the average patch size of patches not known to be used in this study. These patch sizes were then compared in an analysis of variance (ANOVA) to illustrate between season differences.

Patch context was determined by taking the road frontage measurement for the focal patch and combining it with the open habitat complexes it was embedded in. Focal patches were considered to be embedded within open landscapes if they were adjacent to additional open patches. The occupation rate was then calculated using agricultural patches as the sample unit with the number of occupied patches divided by the total number of patches. Patches were considered to be isolated if they were separated from other open patches by at least 500 m. Two additional categories were compared with isolated patches including those complexes with 1-2 km road frontage and agricultural patches embedded within other patches with a total road frontage greater than 2 km. Occupation rate was then compared to patch size as it related to the patch complex (isolated, 1-2 km road frontage, > 2 km road frontage) for both winter and migration.

Landscape Use

Influence of landscape compositon on occupation rate of kestrels during winter (N = 3 survey rounds) and migration (N = 4 survey rounds) were determined for each survey segment (number of surveys in which birds were detected divided by total surveys). A one-way ANOVA compared the seasons based on landscape composition category classes (< 0.4, 0.4-0.49, 0.5-0.59, 0.6-0.69, > 0.7) that were based on the proportion of open habitat (agricultural + idle grass + residential + pasture). One-way ANOVAs also demonstrated the influence of landscape composition on American Kestrel density during winter and migration.

RESULTS

Coastal Population

A total of 463 observations of kestrels were recorded over the study period. Mean density during winter was 0.26 $\pm$ 0.030 (mean $\pm$ SE) observations/100 ha for all habitats sampled combined and 0.41 $\pm$ 0.046 observations/100 ha for open habitats (agriculture + pasture + residential + idle grass). Similar densities were recorded for the spring (0.34 $\pm$ 0.041 and 0.64 $\pm$ 0.091 for total and open densities respectively) and fall (0.19 $\pm$ 0.040 and 0.35 $\pm$ 0.077 for total and open densities respectively) migration periods. Birds were detected within 60 of 86 (69.8%) segments in winter, 55 of 86 (64.0%) segments in spring, and 42 of 86 (48.8%) segments in fall. During the two migration periods combined, kestrels were detected within 62 of 86 (72.0%) segments. In summer, far fewer birds were observed, with a density of 0.035/100 ha for all habitats and birds being detected in only 3 of 86 (3.5%) segments. Because of low sample size, summer birds are excluded from comparative statistical calculations.

Of 453 birds where sex could be determined, 267 (58.9%) were male and 186 (41.1%) were female. Sex ratio (119:69 males to females) was significantly skewed to males during the winter period ($X^2 = 13.3$, df = 1, $p < 0.05$). Overall, sex ratio (95:58) was also male biased during spring migration ($X^2 = 9.0$, df = 1, $p < 0.05$). However, this pattern was driven by the early survey where males were decidedly more numerous (59:22) than females ($X^2 = 16.9$, df = 1, $p < 0.001$). During the late spring survey, males and females were detected with equal frequency (36:36). No sex bias (49:43) was detected during the fall migration period ($X^2 < 0.4$, df = 1, $p > 0.05$).

Habitat Use

The 600 m-wide band transects included along survey routes incorporated a total area of more than 25,000 ha. Land cover within transects was dominated by forest (38.3%), active agriculture (35.6%), residential (9.7%), and pasture (7.8%) (Table 2). Remaining habitats accounted for less than 9% of the total land area. By design, the amount of open lands varied considerably between segments (Figure 3). Fifty-five of the 86 segments selected had more than 50% of their total land cover in open habitats.

Within the range of parameters utilized in this study, male and female kestrels exhibited similar patterns of habitat use during all seasons (all X^2 statistics < 10.0, df = 6, p-values > 0.05). For this reason, sexes were combined in order to evaluate general patterns of habitat use. Similarly, the use of land cover types did not differ between the spring and fall migration periods ($X^2 = 12.3$, df = 6, $p > 0.05$). Spring and fall survey periods were combined in order to allow comparison of habitat use for birds between winter and migration.

Kestrels did not use land cover types according to their availability along survey segments (Figure 4). Kestrels showed significant ($X^2 > 12.5$, df = 1, $p < 0.001$) positive deviations from expected for both agriculture and idle grass and significant ($X^2 > 7.5$, df = 1, $p < 0.001$) negative deviations for pasture, forest, and 'other' habitats. Clear-cuts and residential areas were used according to their relative availability ($X^2 < 3.0$, df = 1, $p < 0.05$). Patterns of habitat use were statistically indistinguishable between winter and migration periods ($X^2 = 4.5$, df = 6, $p > 0.05$).

Table 2. Summary of habitat availability along survey segments (N = 86). All area values are presented in hectares. Open area was calculated as agriculture + pasture + idle grass + residential.

Habitat Type	Mean $\pm$ SE	Minimum	Maximum	Sum	% of total
Forest	112.4 $\pm$ 4.12	34.6	218.7	9,664.8	38.3
Clear-cut	8.4 $\pm$ 1.45	0.0	96.2	723.6	2.9
Agriculture	104.4 $\pm$ 4.46	0.0	186.2	8,976.0	35.6
Pasture	22.8 $\pm$ 2.53	0.0	97.0	1,964.0	7.8
Idle Grass	6.2 $\pm$ 0.65	0.6	29.6	534.2	2.1
Residential	28.6 $\pm$ 1.77	4.6	107.5	2,455.8	9.7
'Other'	10.8 $\pm$ 0.88	2.0	48.5	928.7	3.7
Open	161.9 $\pm$ 4.81	43.6	268.5	13,929.9	55.2
Total	293.6 $\pm$ 2.64	213.6	354.2	25,247.0	-----

Figure 3. Frequency distribution of survey segments (N = 86) based on the proportion of total area in open habitat. Composition is calculated as (area in open habitat)/(total habitat) where open is defined as agriculture + idle grass + residential + pasture.

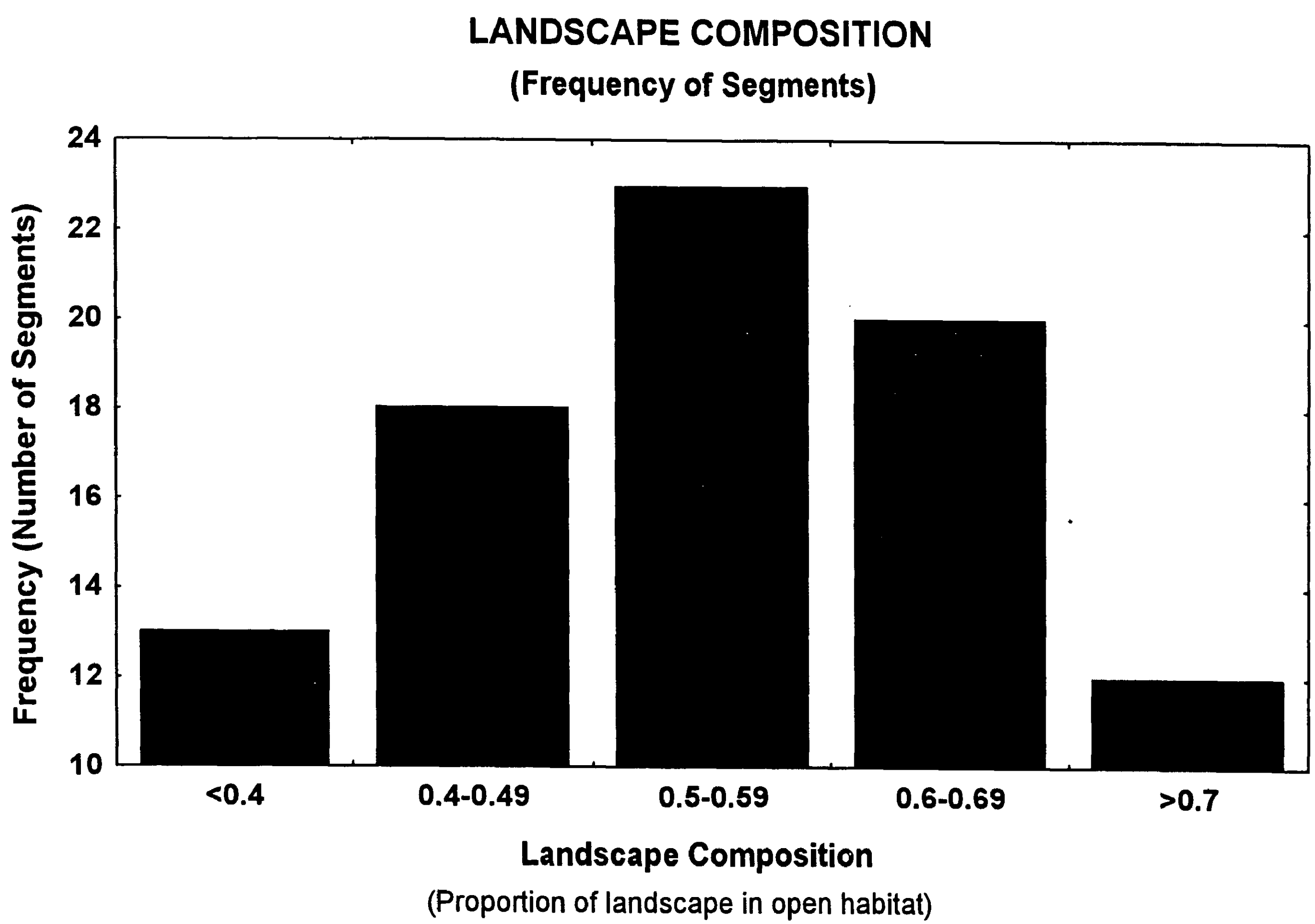
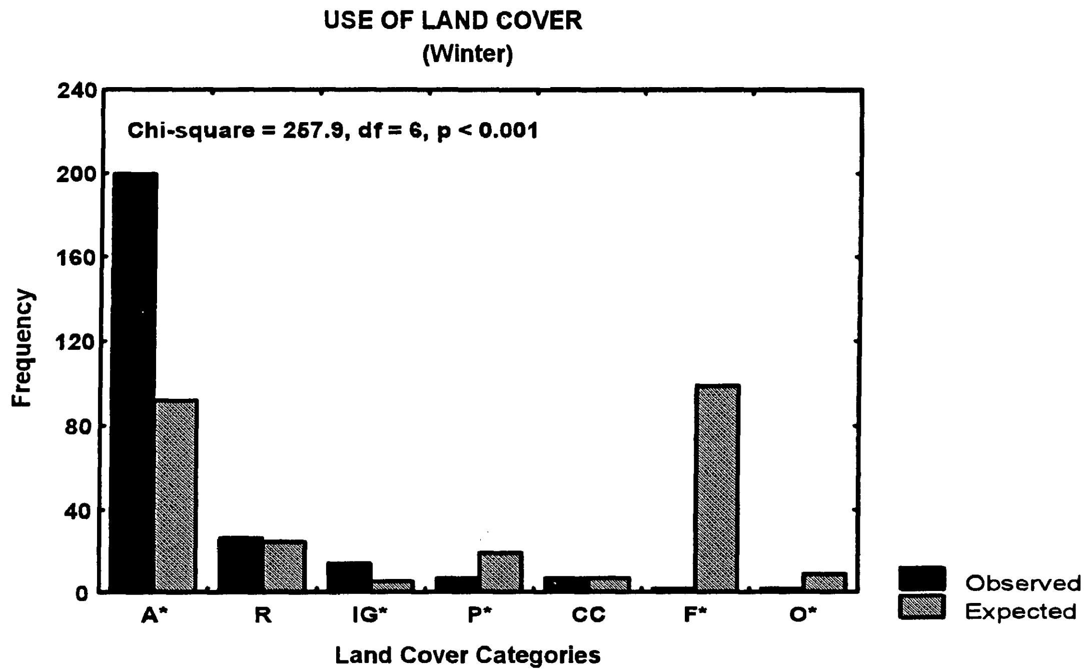
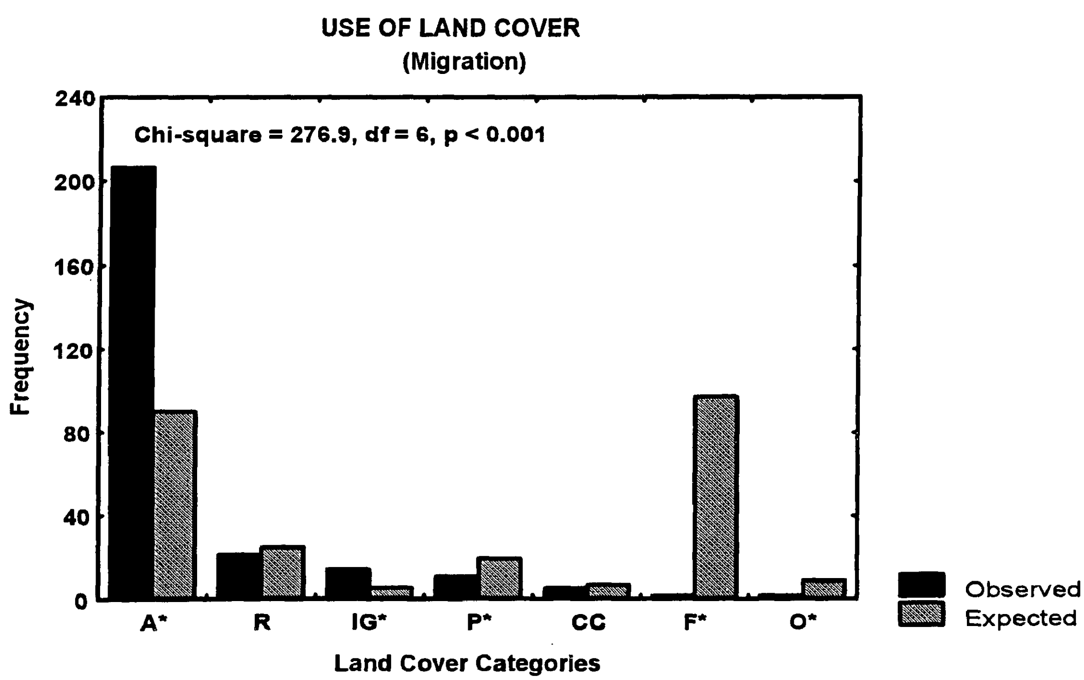

LANDSCAPE COMPOSITION
(Frequency of Segments)
Frequency (Number of Segments)
24
22
20
18
16
14
12
10
<0.4
0.4-0.49
0.5-0.59
0.6-0.69
>0.7
Landscape Composition
(Proportion of landscape in open habitat)

Figure 4. Frequency distribution of kestrel observations among land cover types. Expected values are based on the relative availability of land cover types (see Table 2). Land cover abbreviations are as follows: A = agriculture, R = residential, IG = idle grass, P = pasture, CC = clear-cut, F = forest, and O = 'other'. * indicates that use of land cover type shows a significant deviation from expected values.


USE OF LAND COVER
(Winter)
Chi-square = 257.9, df = 6, p < 0.001
Frequency
240
200
160
120
80
40
0
A*
R
IG*
P*
CC
F*
O*
Land Cover Categories
Observed
Expected


USE OF LAND COVER
(Migration)
Chi-square = 276.9, df = 6, p < 0.001
Frequency
240
200
160
120
80
40
0
A*
R
IG*
P*
CC
F*
O*
Land Cover Categories
Observed
Expected

Patch Use

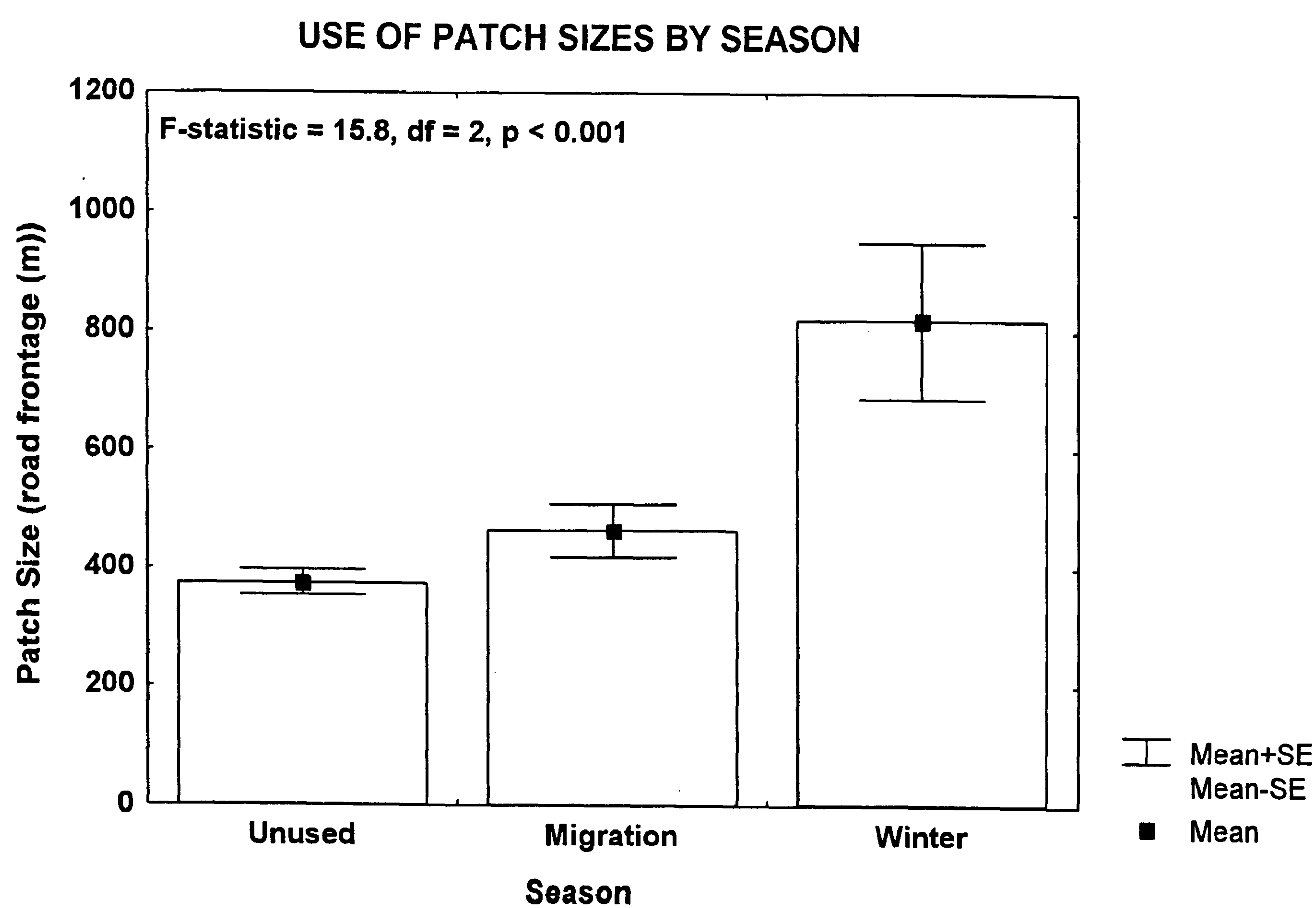
American Kestrels used available, isolated patches of active agriculture differently between seasons (Figure 5). During the winter months, kestrels used isolated patches that were significantly larger on average than those that were: 1) used during the migration periods (F-statistic = 9.98, df = 1, $p < 0.01$) and 2) not known to be used at any time during the study period (F-statistic = 29.97, df = 1, $p < 0.001$). Average patch size was greater than twice as large during the winter as those patches that were not known to be used. Average patch size was not significantly larger during migration compared to those available (F-statistic = 2.56, df = 1, $p > 0.05$), though means indicate some preference for larger patches as compared with those not used.

Patch Context

Landscape context had a significant influence on the use of agricultural patches by American Kestrels during both winter and migration periods (Figure 6). Patches that were embedded within complexes of open lands had significantly higher probabilities of being used compared to isolated patches ($X^2 > 80$, df = 2, $p < 0.001$). Patches that were embedded within large (> 2 km of continuous road frontage) open complexes had the highest probability of being used followed by patches within smaller (1-2 km of continuous road frontage) open complexes. The increase in occupation rate with the type of associated open landscape was similar between seasons.

Although the response of kestrels to changes in landscape composition was similar between seasons, the effect was most dramatic for small patch sizes during winter (Figure 7). As also indicated in Figure 6, patches used by winter resident kestrels were larger on

Figure 5. Comparison of average patch size used by American Kestrels during winter and migration. Also presented is average patch size of patches not documented to be used during the study period.



USE OF PATCH SIZES BY SEASON
F-statistic = 15.8, df = 2, p < 0.001
Patch Size (road frontage (m))
1200
1000
800
600
400
200
0
Unused
Migration
Winter
Season
Mean+SE
Mean-SE
Mean

Figure 6. Influence of landscape context on occupation rates of American Kestrels during winter and migration. Occupation rates calculated using agricultural patches as the sample unit (number of occupied patches/total number of patches). Isolated patches refer to those patches more than 500 m from other open patches. The 1000-2000 category refers to agricultural patches embedded within other patches that collectively had continuous road frontage of 1-2 km. The >2000 category refers to agricultural patches embedded within other patches that collectively had continuous road frontage of more than 2 km.

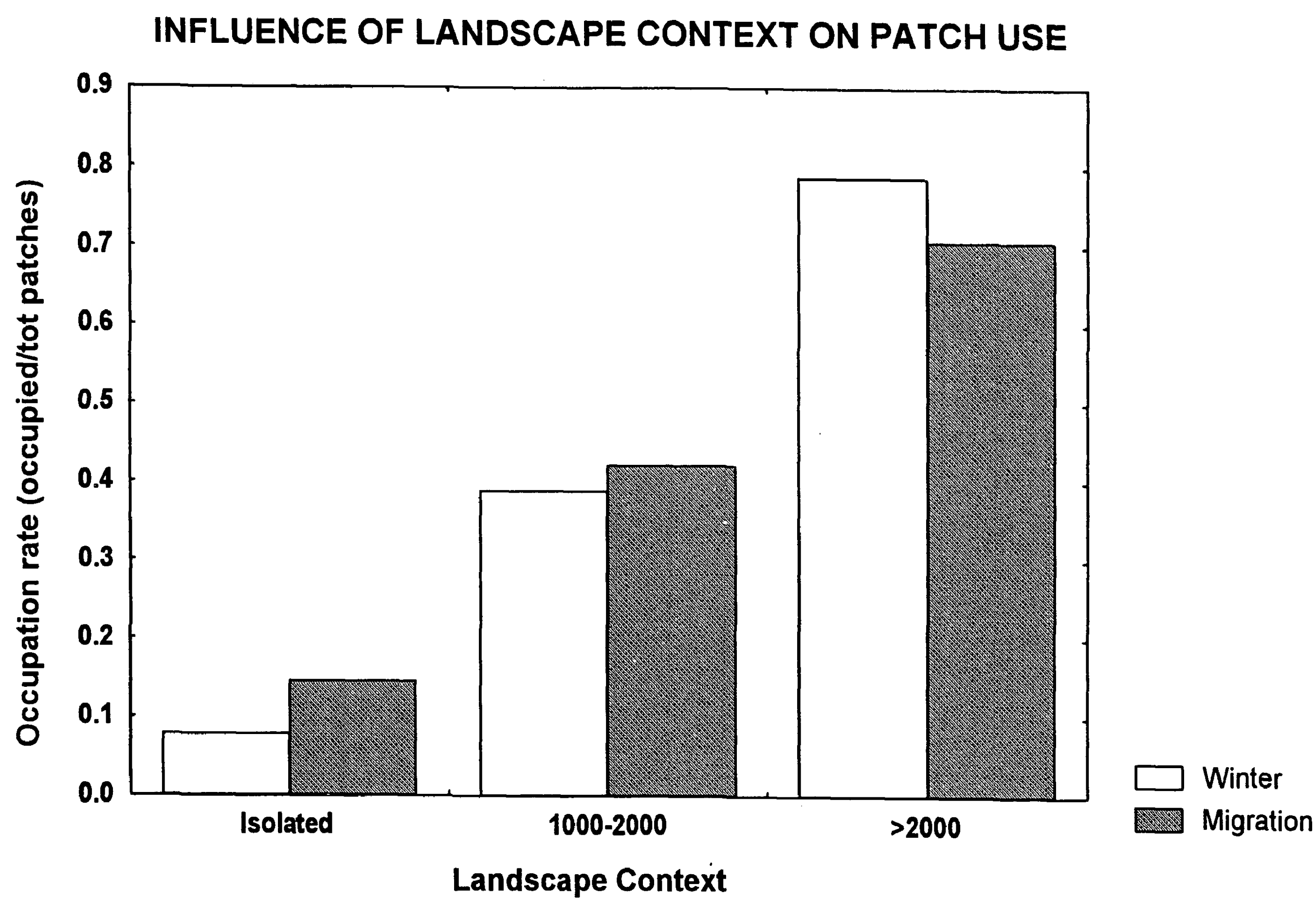
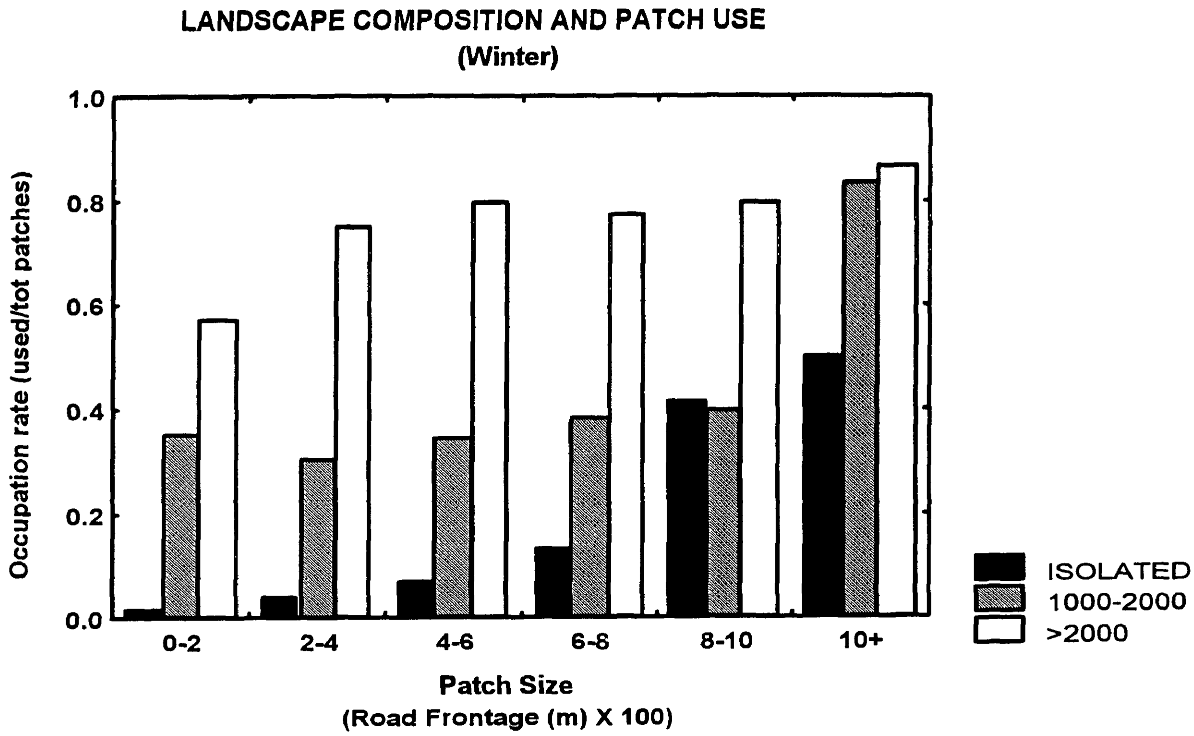
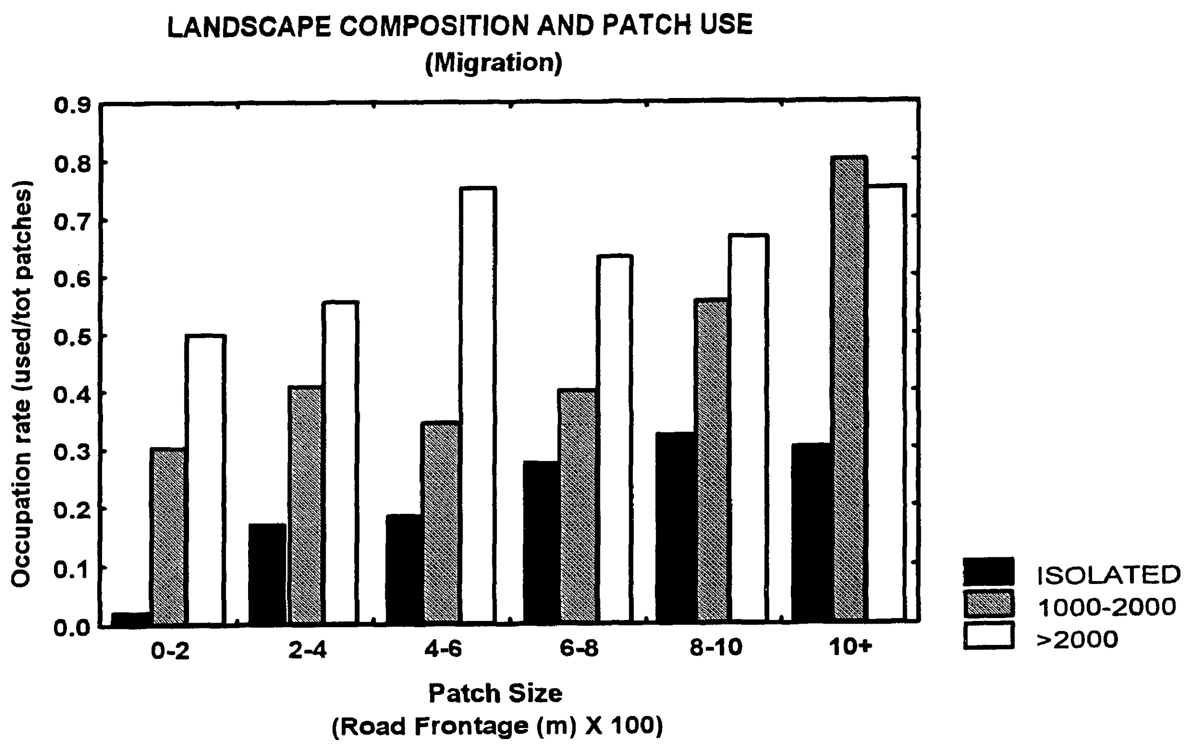

INFLUENCE OF LANDSCAPE CONTEXT ON PATCH USE
Occupation rate (occupied/tot patches)
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Isolated
1000-2000
>2000
Landscape Context
Winter
Migration

Figure 7. Influence of landscape context on occupation rates of American Kestrels across a range of agricultural patch sizes during winter and migration. Occupation rates calculated using agricultural patches as the sample unit (number of occupied patches/total number of patches). Isolated patches refer to those patches more than 500 m from other open patches. The 1000-2000 category refers to agricultural patches embedded within other patches that collectively had continuous road frontage of 1-2 km. The >2000 category refers to agricultural patches embedded within other patches that collectively had continuous road frontage of more than 2 km.


LANDSCAPE COMPOSITION AND PATCH USE
(Winter)
Occupation rate (used/tot patches)
1.0
0.8
0.6
0.4
0.2
0.0
0-2
2-4
4-6
6-8
8-10
10+
Patch Size
(Road Frontage (m) X 100)
ISOLATED
1000-2000
>2000


LANDSCAPE COMPOSITION AND PATCH USE
(Migration)
Occupation rate (used/tot patches)
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
0-2
2-4
4-6
6-8
8-10
10+
Patch Size
(Road Frontage (m) X 100)
ISOLATED
1000-2000
>2000

average compared to migrant kestrels. Winter resident kestrels were rarely observed in isolated agricultural patches with road frontage of less than 800 m. These small isolated patches were used with greater frequency during the migratory period. Although birds select large open complexes in both seasons, this tendency appears stronger in winter.

Landscape Use

Using survey segments as samples, occupation rates increased during both winter and migration with the proportion of the land cover along survey routes that was represented by open habitats (Figure 8). During the winter period, this positive relationship was significant (one-way ANOVA, F-statistic = 10.94, $df = 4$, $p < 0.001$). Occupation rates were very low along survey routes that had less than 60% of associated lands in open habitats. Occupation rates were greater than 50% for survey routes where open habitats accounted for more than 60%. Occupation rates were very high when landscape composition exceeded 70%. During the migration periods, occupation rates exhibited a positive trend with increasing amounts of open land cover. However, this relationship was not statistically significant (one-way ANOVA, F-statistic = 2.06, $p > 0.05$).

Landscape composition had a similar influence on the average density of American Kestrels observed along survey routes as that observed for occupation rates (Figure 9). During the winter period, kestrel density exhibited a significant positive response across the landscape gradient. Average density was more than twice as high along survey routes where land cover represented 70% of the landscape compared to landscapes that

Figure 8. Influence of landscape composition on occupation rates of American Kestrels during winter and migration. Occupation rates were calculated for each survey segments (number of surveys where birds were detected/total surveys) during winter (N = 3 survey rounds) and migration (N = 4 survey rounds). Landscape composition classes were based on the proportion of land cover along survey segments that was in open habitat (agriculture + idle grass + residential + pasture).

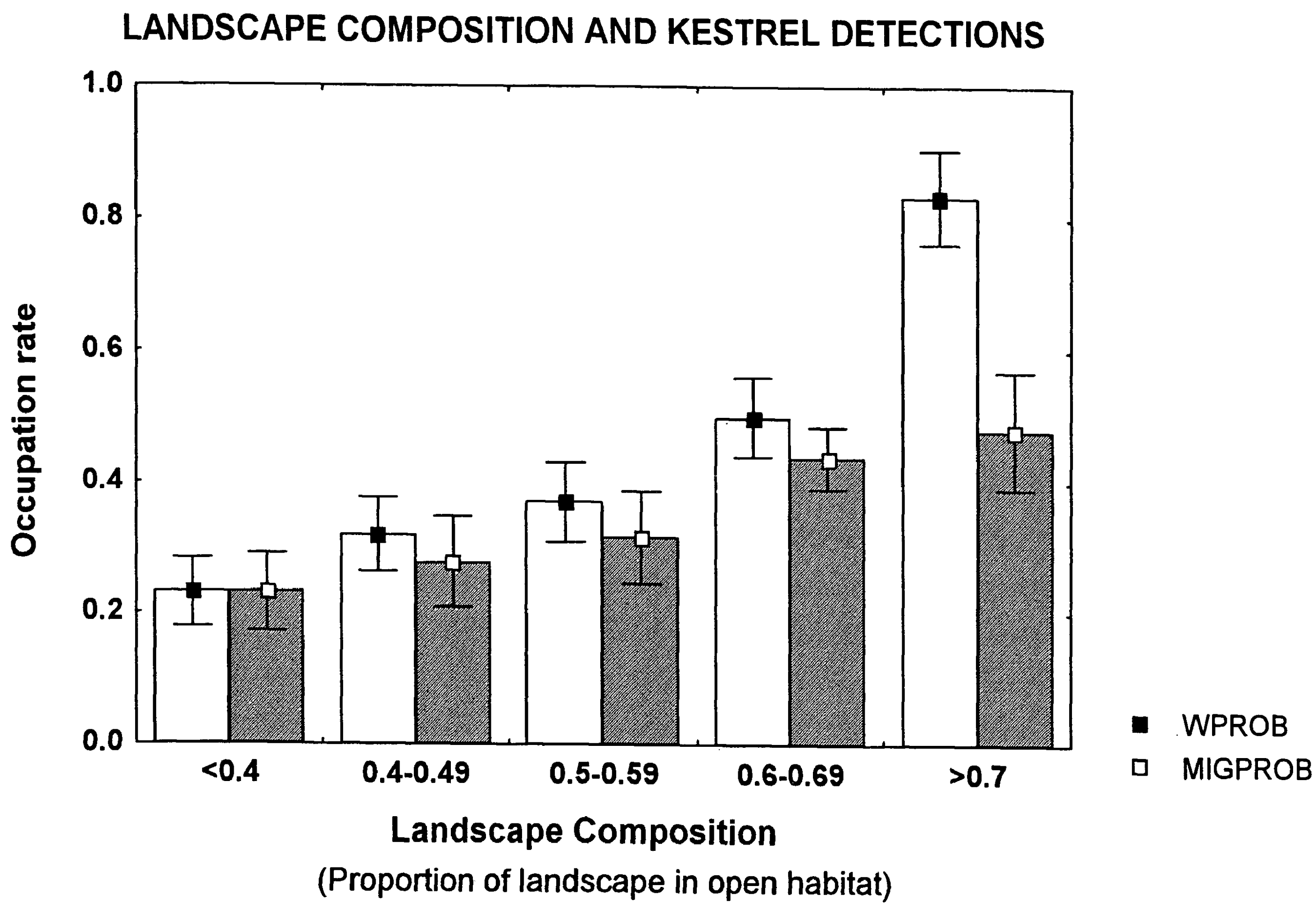
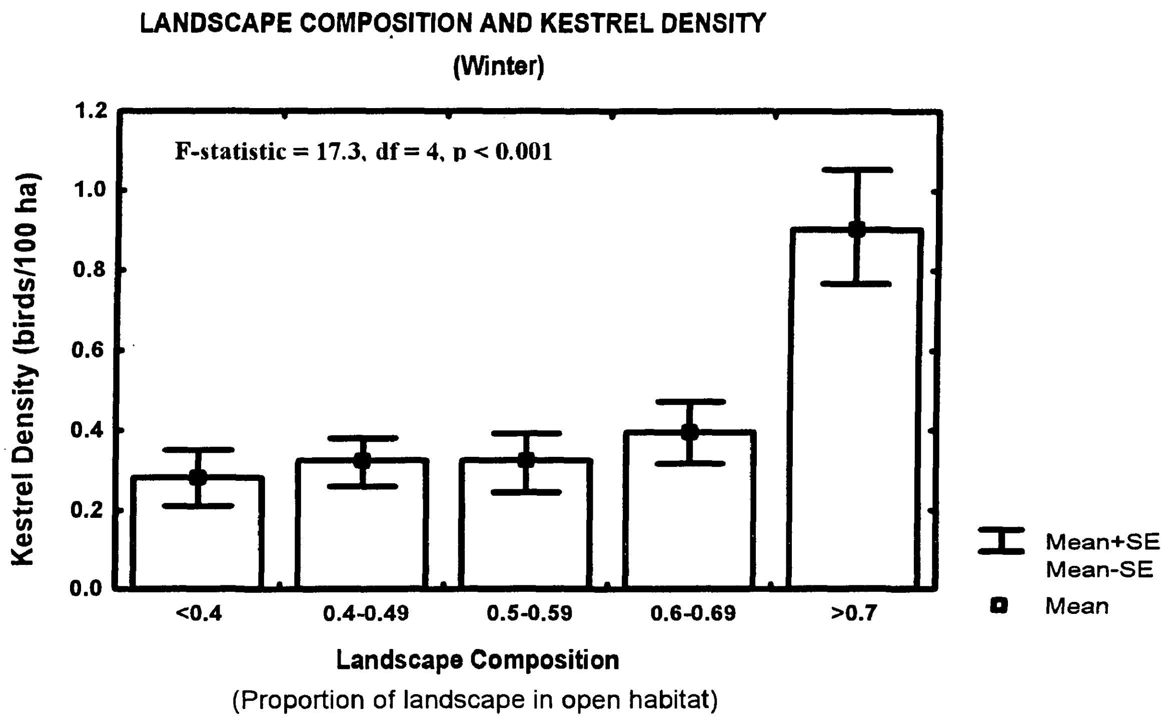
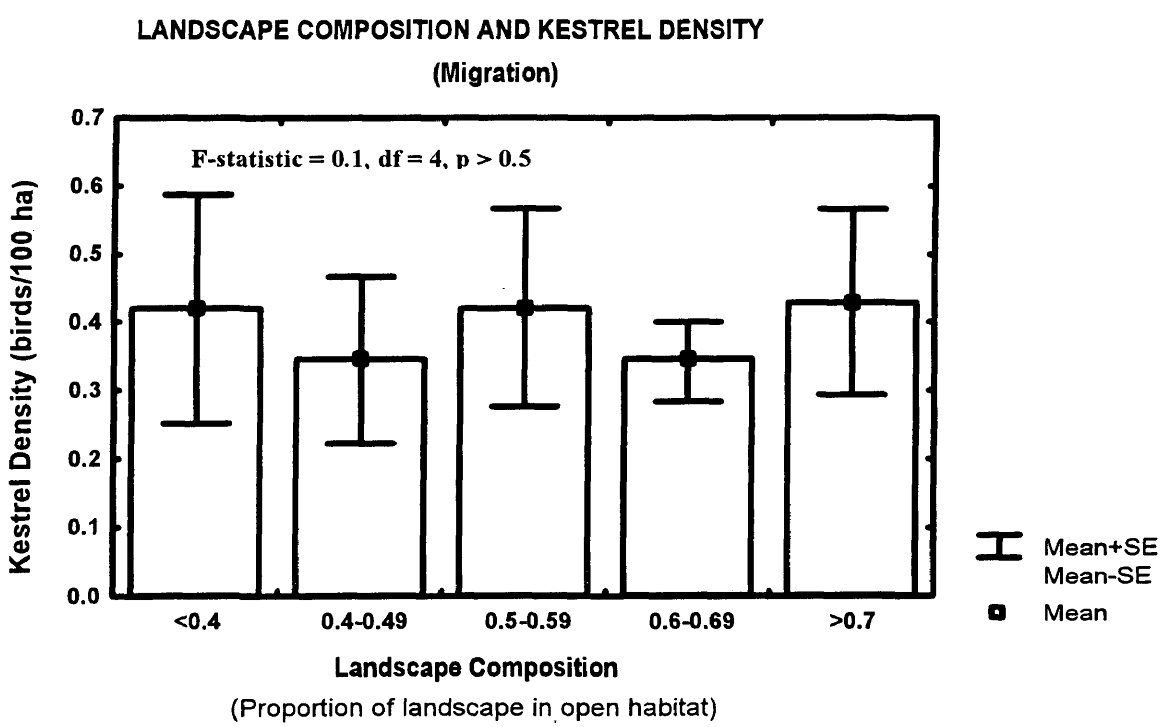

LANDSCAPE COMPOSITION AND KESTREL DETECTIONS
Occupation rate
1.0
0.8
0.6
0.4
0.2
0.0
<0.4
0.4-0.49
0.5-0.59
0.6-0.69
>0.7
Landscape Composition
(Proportion of landscape in open habitat)
WPROB
MIGPROB

Figure 9. Influence of landscape composition on the density of American Kestrels during winter and migration. Landscape composition classes were based on the proportion of land cover along survey routes that was in open habitat (agriculture + idle grass + residential + pasture).



LANDSCAPE COMPOSITION AND KESTREL DENSITY
(Winter)
F-statistic = 17.3, df = 4, p < 0.001
Kestrel Density (birds/100 ha)
1.2
1.0
0.8
0.6
0.4
0.2
0.0
<0.4
0.4-0.49
0.5-0.59
0.6-0.69
>0.7
Landscape Composition
(Proportion of landscape in open habitat)
Mean+SE
Mean-SE
Mean



LANDSCAPE COMPOSITION AND KESTREL DENSITY
(Migration)
F-statistic = 0.1, df = 4, p > 0.5
Kestrel Density (birds/100 ha)
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
<0.4
0.4-0.49
0.5-0.59
0.6-0.69
>0.7
Landscape Composition
(Proportion of landscape in open habitat)
Mean+SE
Mean-SE
Mean

were forest-dominated. Average density within the migration periods showed no detectable trend across the landscape gradient.

DISCUSSION

Density

Mean open habitat densities of the present study over all four seasons were 0.36/100 ha or 21.5 birds/100 km. Mills (1976) collected data on kestrels in south Texas, southern California, Mexico, Arizona, Colorado, and New Mexico over a two-year period. Kestrel densities in major open habitats (includes agriculture, desert, and grasslands) were considerably less than the present study, with 12 birds/100 km across all seasons. In the present study, bird densities varied among migration periods, but for each a greater density was observed in open habitat than across all habitats. Densities were 0.34/100 ha for all habitats and 0.64/100 ha for open habitat in spring, and 0.19/100 ha and 0.35/100 ha in fall. A total of 245 birds were observed during the migration periods with 33% in spring and 19.9% in fall.

During winter surveys, a total of 188 kestrels were observed within 69.8% of the 86 survey segments. Wintering kestrel density was 0.26/100 ha for all habitats and 0.41/100 ha of open habitat. This is 37% greater than reported in a study of wintering raptors in Kentucky, where kestrels were observed at 0.19/100 ha for all habitats by Sferra (1984b). In a study in North central Florida (Bohall-Wood and Collopy 1986), 1,433 kestrels were sighted during the one-year study. Eighty-four percent of these occurred during the winter months, representing a large influx of migrants into that area. After controlling for differing survey effort between seasons in the current study, one-third of the birds were observed during the winter months in the coastal plain. The proportion of birds observed during winter and migration was more similar in the current study than the Florida study.

The American Kestrel is one of the most common and widely distributed raptors of the Western Hemisphere (Cade 1982), but significant decreases have been noted in certain areas. It is possible that these declines can be explained by a gradual loss of prime foraging habitats used by both species (Bednarz and Dinsmore 1982, Sferra 1984a) as open pasture and agricultural areas were converted to residential developments. It is unclear what population trends have occurred within the Virginia Coastal Plain over recent years, but it is evident that a much greater number of birds are present in this area in the winter, with only 6.5% of total birds being observed during the breeding season. Kestrels are much less abundant during the breeding season, perhaps because cavity trees for nesting are in short supply in areas with sufficient foraging habitat and are used by multiple bird species. All summering kestrels observed on surveys were nesting in artificial cavities in manmade structures.

Sex Ratio

Overall sex ratio for the entire study was 267 (58.8%) males and 186 (41.1%) females, which is almost identical to the 58:42% ratio found based on continent-wide Christmas Bird Count data (Arnold 1991). However, when the data is broken down by season, the sex ratio was significantly skewed to males during the winter months, 119 (63.3%) males compared to 69 (36.7%) females. Sferra's study (1984a) on wintering kestrels in Madison County, Kentucky, found a remarkably similar ratio with 58% males and 42% females, which may indicate some relationship of sex ratio to latitude. Several authors have described an unbalanced sex ratio in favor of females in wintering kestrels. Koplin (1973) found a prevalence of females, with females in some areas of Northern California outnumbering males by 6 to 20 times. For the most part, these findings were a localized effect found in conjunction with differential habitat preference. Collopy (1973) was unable to compare male and female prey preference at Arcata Bottoms in Northern California, since so few males were observed and females outnumbered them 9 to 1.

In the current study, ratios in the spring were also male-biased, but this pattern was driven by the earlier of the 2 surveys with 59 males to 22 females. During the second survey round in spring, migration numbers of males and females detected were equal (36:36). This would coincide with other studies (Roest 1957; Smith *et al.* 1972) that show males moving through earlier during spring migration. No sex bias was detected during fall migration (49:43); this contrasts with findings by Stotz and Goodrich (1989) at Hawk Mountain, Pennsylvania, where kestrels showed a differential migration pattern with females preceding males by 11 days. Smallwood's (1988) findings support a differential return to winter habitat by reporting that males arrive later on territories in south central Florida. His data also indicate a ratio of 52.4% males to 47.6% female during fall migration based on banding data compiled from 1960-1984.

Habitat Use

Significant deviations of habitat patch use from availability were detected in the Coastal Plain (Figure 4). Agriculture and idle grasslands were used at a greater than predicted rate while pasture, forest, and 'other' habitats were used at a lesser than predicted rate during all seasons. Residential and clear-cut areas were used as predicted based on the amount of that habitat available. The reason pasture was utilized less than expected may be due to a lack of perching sites from which birds can forage as compared to other types of open habitat. Grazing of pasturelands might also reduce prey density by reduction of ground cover. Clear-cut was used as expected based on availability, rather than less often as hypothesized. Although this type of open habitat is likely not of high quality when compared with other open habitat types due to the greater difficulty in spotting and pursuing prey in woody detritus, kestrels use clear-cut areas more than forested areas despite their relative lack of availability.

Sex-specific Habitat Use

Male and female kestrels exhibited similar patterns of habitat use during all seasons. This is an unusual finding based on the current literature, as most studies have shown differential habitat use between males and females. Several previous studies have found females to use more open areas such as agricultural fields and large pastures while males use smaller pastures, woodlots, and orchards (Koplin 1973; Collopy 1973; Mills 1975,1976; Stinson *et al.* 1981; Bohall-Wood and Collopy 1986; Smallwood 1987). Theories as to why differential habitat use might exist have included: 1) character displacement reduces intersexual competition for food resources (Koplin 1973), 2) the female dominance theory, in which larger females force males into sub-optimal habitats for foraging (Mills 1976), 3) males and females possibly prefer different types of prey and occupy separate ecological niches (Bohall-Wood and Collopy 1986), and 4) bimodal migration allows females to occupy the highest quality territories first due to earlier arrival on the wintering grounds (Smallwood 1988).

It is interesting that these studies of wintering territories showed such a strong segregation in habitat use patterns while in the Coastal Plain males and females showed no significant difference in habitat use during the winter months. This discrepancy with the literature may be due to the fact that this study was done at a much broader spatial scale than many previous studies, in which habitat was analyzed within areas less than 60 m around each bird. However, the current findings do concur with Sferra's study (1984a) in Madison County, Kentucky, where sex-specific differences in habitat were not significant. This could indicate a latitudinal effect on sex-specific habitat use.

The use of land cover types by males and females did not differ among spring and fall migration periods and winter. None of the previous literature looks at habitat use during migration, most likely due to the limited amount of time to observe birds as they move through to winter and summer territories. Bohall-Wood and Collopy (1986) found that although the sexes used habitat differentially during winter months, there was no sexual difference in habitat preference during the summer months. The finding that migrating male and female kestrels choose similar habitat is not surprising and is probably due to the rapidity with which they move from one area to another.

Patch Use

Size of patches utilized by kestrels was significantly different between wintering and migrating birds (Figure 5). The average size of agricultural patches used was significantly larger during winter than either those patches used during migration or those patches found not to be occupied during the entire course of the study. Patch size used in winter was approximately twice that of patches not used. Although patch size occupied during migration was larger than that of unoccupied patches, this difference was minor and lacked statistical significance. Taken as a whole, these data indicate that American Kestrels are more selective in their choice of territory during the harsh winter months, when prey would presumably be less abundant than during migration, a much shorter period of occupation with a greater abundance and variety of prey items. During all seasons, kestrels chose habitat patches of greater area than predicted from the range of sizes available, but the degree of selectivity was greatly amplified during the winter season. This dichotomy has not been previously demonstrated for this species but follows logically from the length of use of habitat and foraging demands of individuals under these very different seasonal conditions.

Patch Context

Landscape context, as determined by occupation rate in relation to size of open habitat frontage areas, had a significant influence on the use of agricultural patches during all three seasons (Figures 6 and 7). Patches imbedded within open land were used with greater frequency than isolated patches. There was a trend of use from larger (> 2 km) to smaller (1-2 km) frontage areas during both seasons. This effect was most dramatic when comparing winter residents to migrating kestrels, as tendency to use large open complexes and avoidance of isolated patches were significantly greater during the winter. Few wintering kestrels were sighted in isolated agricultural patches with frontage < 800 m and even fewer in patches with frontage of < 400 m, despite the relative abundance of isolated patches. Small isolated patches were used with some frequency during migration, supporting the idea that wintering kestrels are more selective in their habitat use than ephemeral migrants. Landscape composition is clearly a more important cue for kestrels that arrive for an extended stay rather than for birds simply moving through an area. Both average sizes of patches used and their degree of fragmentation and isolation as measured by extent of frontage correlate significantly with occupation rate. Wintering kestrels show a degree of selectivity for landscape composition at the local scale not previously demonstrated.

Landscape Use

There is a clear influence of landscape type on occupation rate among the eighty-six survey segments (Figure 8). When compared with landscape composition and availability across segments (Figure 3), detection of kestrels was much higher in segments with greater than 70% of associated lands in open habitat. There was no significant difference between seasons in use of segments with proportions of open habitat less than 70%, but in segments greater than 70%, the occupation rate is much greater during winter than migration. The trend for greater use as proportion of open habitats increases is significant in winter, being more than twice as large in primarily open segments than largely forested segments, but a similar trend was not observed during migration (Figure 9). This is a large-scale verification of the patterns observed at the local scale and shows that differential habitat choice patterns by American Kestrels are validated at the level of individual segments, survey routes, and the Coastal Plain as a whole.

Conclusion

This study examines the effects of patch size and landscape context on kestrel habitat use across a scale that has not previously been investigated. Preferences of both sexes for habitat coincide with percent open area along with patch size. After taking a closer look at usage based not only on individual patches at the segment level, but across the survey routes and the Coastal Plain as a whole, it will be much easier to understand the landscape needs of this species. This information will be very important in future land management choices as related to kestrels and other birds dependent on large areas of open habitat. It is also important to focus on the birds' needs during the winter and summer months, since this is when the highest demands are placed on the kestrels to defend a territory and maintain enough foraging habitat to survive.

Appendix 1. Location and landscape composition based on the proportion of landscape in open habitat (landscape categories: 1) < 0.4, 2) 0.4 - 0.49, 3) 0.5 - 0.59, 4) 0.6 - 0.69, 5) $\geq$ 0.7) of each of the 86 survey segments.

Survey Route	Road Segments	Location (by County/City)	Landscape Category
1) Eastern Shore	01-Rt.600 starting at Rt.13	Northampton	5
	02-Rt.600 starting at Rt.643	Northampton	5
	03-Rt.600 starting at Rt.632	Northampton	5
	04-Rt.600 starting at Rt.621	Northampton	5
	05-Rt.600 starting at Rt.603	Northampton/Accomack	3
	06-Rt.600 starting at Rt.622	Accomack	4
	07-Rt.13 south from 180	Accomack/Northampton	4
	08-Rt.13 south from Rt.604	Northampton	2
	09-Rt.13 south from Rt.622	Northampton	4
	10-Rt.13 south from Rt.633	Northampton	5
	11-Rt.13 south from 1km past 643	Northampton	5
2) Pungo	01-London Bridge Road from Industrial Park to General Booth Blvd.	Virginia Beach	4
	02-Princess Anne Rd. from Elson Green to just after Vaughn Rd.	Virginia Beach	5
	03-Princess Anne Rd. from Dudley Ct. to Black Water Road	Virginia Beach	3
	04-Land of Promise Road	Virginia Beach/Chesapeake	5
	05-Head of River Road	Chesapeake	5
	06-Morris Neck Road from Princess Anne to ½ km before Shipp's Cabin	Virginia Beach	5
	07-Muddy Creek Road from Gum Bridge to New Bridge Road	Virginia Beach	4
3) Courtland	01-Rt.31 from Rt.630 to Wakefield	Surry/Sussex	3
	02-Rt.620 off of 31, right onto 622	Sussex	1
	03-Rt.606 from 2nd 604 to Rt.724	Sussex	1

	04-Rt.35, starts at farm road after 631 and goes to Sebrell area	Sussex/Southampton	2
	05-Rt.35 from 606(left) onto 58 Bus. Ends at Rt.58	Southampton	2
	06-Rt. 757 off of 58 West, left on 651, left on 609, left on 652	Southampton	4
	07-Rt.650, just before 649 onto 611	Southampton	4
	08-Rt.258, starts 1km after 611 to 609	Isle of Wight	3
	09-Rt.460 from Rt.258 to Zuni	Isle of Wight	2
	10-Rt.620, 3km in from Rt.460	Southampton/Isle of Wight	2
	11-left on Rt.637	Isle of Wight	2
	12-Rt.621 starting at Rt.625	Isle of Wight	3
	13-Rt.626 from 1.2km after end of segment 12	Surry	3
4) Suffolk	01-Rt.617 from 0.6km past Bacon's Castle to Hog Island entrance	Surry	2
	02-Rt.10 east from 676 to 258	Isle of Wight	4
	03-Rt.258 from 709, left onto 637	Isle of Wight	4
	04-Rt.637 from 644 to 603	Isle of Wight	4
	05-Rt.603 from 1km past segment 04	Isle of Wight/Suffolk	2
	06-Rt.632 off of 460, left on 607, left on 644 ending near Cypress Cove Lane	Suffolk	4
	07-Rt.58 west from 738 to 647	Suffolk	3
	08-Rt.647 starting 0.7km past transmission tower after RR crossing	Suffolk	3
	09-Rt.13 north from 677 onto 675 then left onto 32 north	Suffolk	1
	10-Rt.10/32 north from 58 to 125	Suffolk	3
	11-Rt.10/32 north starting at 600(left)	Isle of Wight	3

	12-Rt.17 from Kiln Creek Area to 173 east	York	2
5) James River	01-Rt.10 from Magnolia Circle (trailer park) to Bacon's Castle	Surry	3
	02-Rt.31 south from 10 west to 618	Surry	4
	03-Rt.10 west from 31 to Rt.40	Surry	2
	04-Rt.653 start at Willow Hill onto 611	Prince George	5
	05-Rt.10 west from 625 (Hines Rd) to Jordan Point Road	Prince George	2
	06-Rt.5 from 1.8km before Turkey Island Neck Road to back entrance of Curles Neck Farms	Henrico	3
	07-Rt.5 east from 609(left) to 615	Charles City	4
	08-Rt.5 east from field area before Sherwood Forest to Rt.623	Charles City	1
	09-Rt.614 starting at Jamestown Road	James City	2
	10-Rt.610/603 from Forge Road to Toano	James City	4
6) Fredericksburg	01-Rt.721 from 628(left) to 664	King & Queen	3
	02-Rt.721 from 635 to past 652	King & Queen/Caroline	2
	03-Rt.721 from 0.4km before 646 to 0.6km before 643(left)	Caroline	3
	04-Rt.721 from 717(left) to Rt.2	Caroline	3
	05-Rt.2 starting at 631(left)	Caroline	1
	06-Rt.2 from 606(left) to 609(left)	Caroline/Spotsylvania	1
	07-Rt.3 East from 601 to after 605	Stafford/King George	5
	08-Rt.3 East from RR crossing to nursing home	King George	3
7) Northern Neck	01-Rt.610 from Rt.3 onto Rt.607	King George	4

	02-Rt. 301 from Rt.17 to int. with Rt.3	Caroline/King George	4
	03-Rt.3 from Rt.627 to Rt.204	Westmoreland/King George	1
	04-Rt.3 east starting at Rt.214	Westmoreland	4
	05-Rt.3 east from Rt.600 to Rt.613	Westmoreland	3
	06-Rt.360 from Rt.3 to Rt.607	Richmond	4
	07-Rt.607	Richmond	3
	08-Rt.3 from ½ km past 620 to Rt.607	Richmond	3
	09-Rt.3 from 1034 to Kilmarnock Bridge	Lancaster	1
	10-Rt.3 from 621 towards Saluda	Middlesex	3
	11-Rt.606/614 starting at Rt.615	Gloucester	2
	12-Rt.614 left off of Rt.17 onto 629	Gloucester	4
	13-Rt.216 east off of 17 south	Gloucester	3
8) Middle Peninsula	01-Rt.273 at Barhamsville to West Point	New Kent	2
	02-Rt.30 from 625 to approx. Rt.626	King William	3
	03-Rt.633 off of Rt.30 from just before Rt.621 to Lester Manor	King William	1
	04-Rt.30 from 640 to approx. Rt.648	King William	1
	05-Rt.600 left off of Rt. 30	King William	1
	06-Rt.360 from 667 to approx. Rt.628	King William/Hanover	4
	07-Rt.360 from 611(left) to 631	King William/King & Queen	2
	08-Rt.684 off of 360 to approx. 607	Essex	2
	09-Rt.607 onto 617 left	Essex/King & Queen	1
	10-Rt.631 from 607 onto Rt.14	King & Queen	3
	11-Rt.14 from 602 to 610	King & Queen	2
	12-Rt.33 from Rt.14 to approx. 637	King & Queen/Gloucester	1

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